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Notes on
**Flowering
and
Fruiting**
of Northeastern
Trees

by

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Notes on

Flowering and Fruiting of Northeastern Trees

by

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INTRODUCTION

Most published observations on the flowering and fruiting habits of forest trees have dealt with the periodicity of fruiting in entire species. This is natural since the main reason for making such observations has been the forecasting of seed crops.

In tree-breeding research, however, individual trees are important. The tree breeder would like to know--

- On what date will a tree flower?
- How much variability is there within and between species in flowering and fruiting habits?

¹Stationed at the Morris Arboretum, Philadelphia, in cooperation with the University of Pennsylvania.

- Is size of flower crop a good indicator of size of fruit crop? If not, are there obvious reasons for the discrepancy?
- Is periodicity of male and female flower crops the same?
- What effect does age have on flowering?
- Can flowering and fruiting habits be easily modified by chemical or physical stimulation or by climate?

Observations made in connection with tree-breeding activities of the Northeastern Forest Experiment Station in 1947-51 supply some answers to the first three questions. But only limited information has been obtained on the other three.

For first dates of flowering of a wide variety of trees and shrubs in the Philadelphia area, see Meehan (10).²

Most of the trees studied are located in the Morris Arboretum of the University of Pennsylvania, at Philadelphia, Pa.; on the campus of Haverford College, Haverford, Pa.; at Westtown School, Westtown, Pa.; and in Andorra Nurseries, Conshohocken, Pa. Most of the specimens were planted. Their origins were unknown. All specimens were nearly or completely open-grown.

For some species (red, Norway, and sugar maples; eastern white, Austrian, and Scotch pines; and white and green ash) conclusions as to the proportion of trees that are fruitful were strengthened by casual observations of several hundred specimens in addition to those on which records were kept.

The phenological observations were made each year on the same general population of trees, but were often made--especially in the unfruitful groups--on different individuals. The extent of individual variation and constancy is described under the various genera.

For purposes of record, fruit crops were classified as very heavy, heavy, medium, light, very light, or none. The respective numerical ratings used were 5, 4, 3, 2, 1, and 0.

²Underlined numbers in parentheses refer to Literature Cited, page 37.

The size of a flower or fruit crop was usually estimated from the ground in terms that could be translated into number per branch or tree; and allowances were made for size of tree. The terms "heavy," "medium," and so on, as used to describe a fruit crop, are relative. For example, a crop of 100 acorns from a large oak might be a medium fruit crop to a nurseryman who needs 100 acorns, a light crop to a forester who needs a bushel, and a very light crop to a tree-breeder who spent 2 weeks bagging thousands of flowers.

Some of the observations may be inadequate in that the sample was not a representative cross-section of the species. There were several instances in which differences in flowering were suspected to be due to racial origin; there may be others in which lack of flowering is an attribute of race rather than species.

MAPLE

(*Acer*)

Flowering Habits

Grant (5) has pointed out the importance of pollination method as an isolating mechanism in angiosperms. Some 40 percent of the diagnostic characters that differentiate species are found in the flower in bee-pollinated plants. In plants pollinated by other insects, 15 percent of the diagnostic characters are found in the flower; in wind-pollinated plants only 4 percent.

The maples provide a good illustration of this tendency. They are primarily bee-pollinated, and nearly all species are well differentiated in floral characters as well as in foliage and growth characters. This diversity of floral characters is evident not only in the structure of the flower and inflorescence, but also in differences in time of flowering and in tendencies toward dichogamy and dioeciousness.

In most maple species the flowers are structurally perfect. However, in the species observed the flowers were never functionally perfect. If the pistil was functional the anthers failed to dehisce, even though they might be nearly as large as functional anthers. Conversely, the pistil was either lacking or was very small and nonfunctional in the male flowers.

Section Platanioidea is the most primitive (6). Acer platanoides³ is typical. Its flowers have calyx, corolla, stamens, and pistil. In female flowers the anthers become nearly full-sized, although they are nonfunctional; and the pistil is 5-6 mm. long. In male flowers the pistil is only 1-2 mm. long. The trees are monoecious. There is nearly complete dichogamy (16), with little overlapping of male and female flowering periods. Each flowering period lasts 2-4 days, and the tree flowers over a period of 1-2 weeks.

Other species in the section have similar flower and inflorescence structures. The single trees available of three other species had successive flowering periods that were entirely male. The dichogamy pattern found in A. platanoides was also typical of A. buergerianum (Section Spicata) and of A. palmatum and A. japonicum (Section Palmata).

Even in a dichogamous species like A. platanoides there is a slight tendency toward dioeciousness: 3 of 32 trees observed produced nothing but male flowers in each of 5 years.

In A. saccharum (Section Saccharina) flower reduction has progressed farther: the corolla has been lost. Dichogamy is very incomplete and natural selfing is probable on most trees. At least in the Philadelphia area there is a pronounced tendency toward dioeciousness, for most of the trees there produce only male flowers or male flowers with a few female flowers.

In A. rubrum and A. saccharinum (Section Rubra) there is a tendency toward dioeciousness rather than toward dichogamy. The majority of trees observed are purely male or female--although some had both types of flowers. The flowers remain structurally perfect, although A. saccharinum has lost its corolla. The inflorescence has been reduced much, to four or five flowers. In these species all flowers on a tree are within a day or so of each other in stage of development, and the probable receptive period for individual trees lasts from a few days to a week.

Reduction of flower parts is also strongly pronounced in A. negundo (Section Negundo). There is complete dioeciousness, the corolla is lacking, the calyx is very small, and male and female flowers contain no rudimentary parts of the opposite sex. All flowers on a tree are at nearly the

³Nomenclature in this report follows Rehder (14).

same stage of development at any one time. Pollen-shedding lasts about 4-8 days for individual trees, and the period of receptivity lasts about twice as long on female trees. In A. henryi the flowers are similarly reduced, and pollen-shedding lasts a week or more on individual trees.

In A. saccharum there was a noticeable localization of the female on certain portions of the tree crown, other branches being wholly male. In monoecious trees of A. rubrum and A. saccharinum there was also a tendency for the male and female flowers to be localized on certain branches, although an intimate mixture of the two kinds is found sometimes on A. rubrum. In other species flowering was similar over the entire crown.

Effect Of Age

Most of the male specimens observed were 1 foot or more in diameter, and presumably well past the minimum size for flowering. Data on this point are available only for A. rubrum, some of which flowered the fourth year from seed.

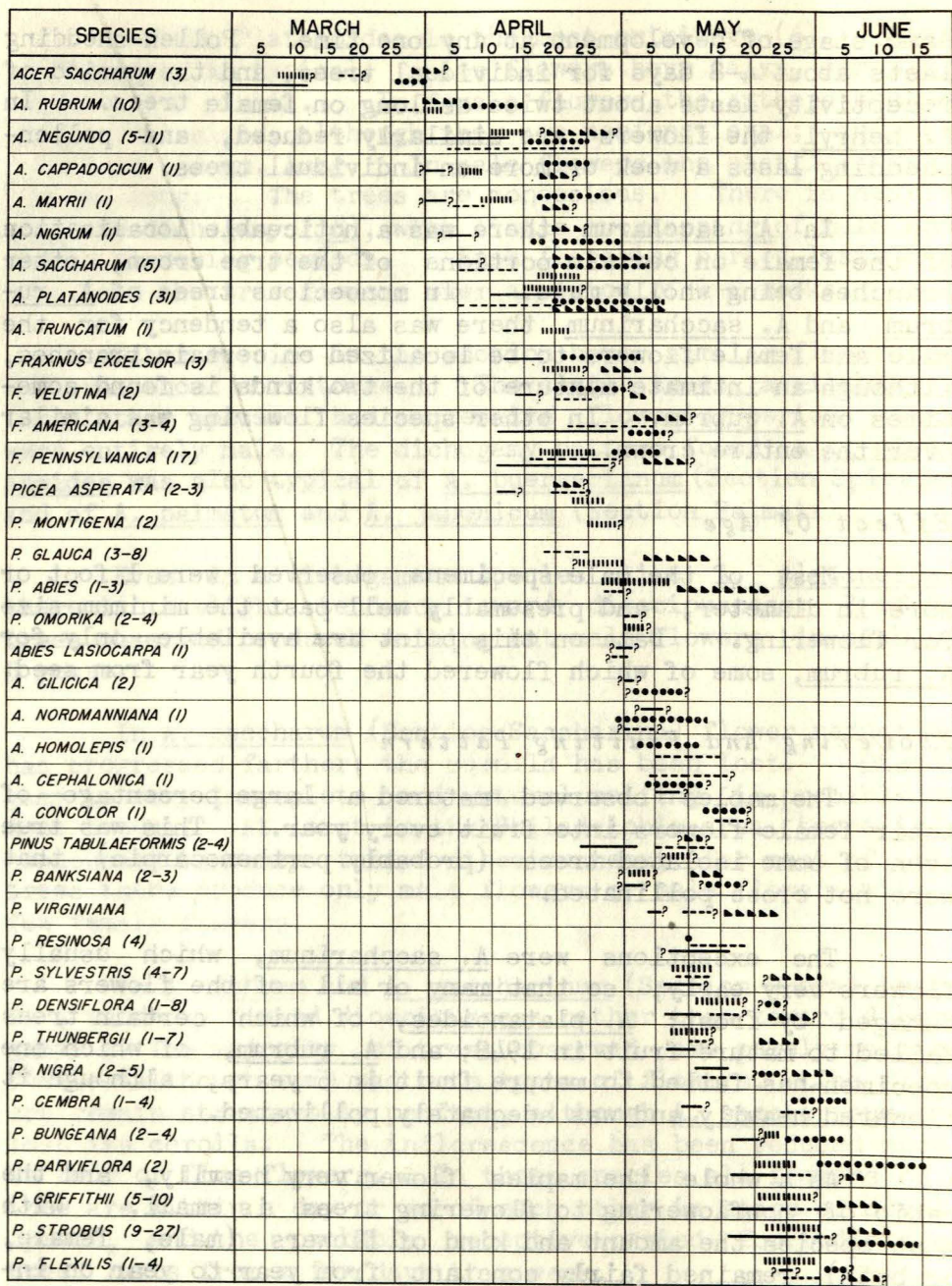
Flowering And Fruiting Pattern

The maples observed matured a large percentage of their female flowers into fruit every year. This was true even of some isolated trees (probably parthenocarpic) that were not cross-pollinated.

The exceptions were A. saccharinum, which usually flowers very early, so that many or all of the flowers are damaged by frost; A. platanoides, of which certain trees failed to mature fruit in 1948; and A. rubrum, of which one specimen has failed to mature fruit in 5 years, although it flowered heavily and was adequately pollinated.

As a whole the maples flower very heavily, and the ratio of nonflowering to flowering trees is small. With most species the amount and kind of flowers (male, female, or both) remained fairly constant from year to year on individual trees--and often on portions of individual trees. So not only the amount of flowering but also the amount of fruiting per tree was about the same from year to year.

A. saccharum is not constant in producing female flowers. Two of 47 trees observed produced female flowers 3 years out of 4; half the trees produced no female flowers; and the rest produced female flowers only in 1950 or in 1950 and one other year. Data on constancy of male flower set are lacking, but it is known that at least three trees pro-



..... 1947 - - - - - 1948 ——— 1949 ▲▲▲▲▲ 1950 ||||| 1951

Figure 1.--Duration of female receptivity or pollen-shedding of trees in the Philadelphia area. Numbers in parentheses indicate number of trees the records are based on.

duced male flowers every year. Judging from the difficulty in finding female flowers suitable for bagging and observation, the ratio of male to female flowers apparently is not less than 10 to 1, and it is probably closer to 50 to 1.

A. platanoides was less variable. Nearly all trees flowered every year, and the size of the flower crops varied by 50 to 75 percent. Observation of 32 trees for 5 years indicates that the ratio of male to female flowering periods is about 2 to 1: there were 243 male periods and 127 female periods in that time.

There are some data for a few other species. Two specimens of A. henryi flowered heavily male in all years. Two specimens of A. buergerianum flowered heavily every year, both male and female. And one specimen each of A. mayrii and A. cappadocicum flowered heavily male every year.

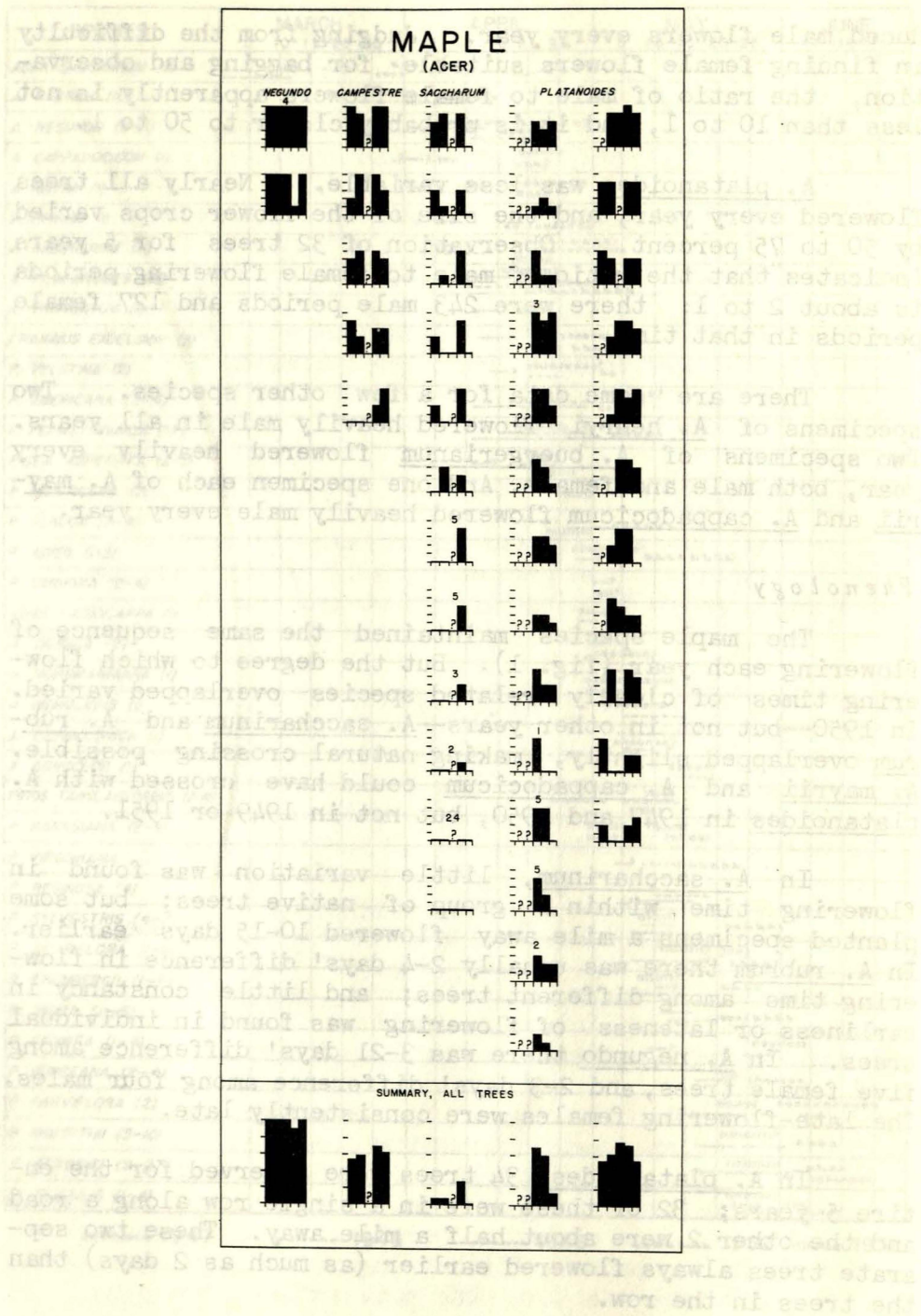
Phenology

The maple species maintained the same sequence of flowering each year (fig. 1). But the degree to which flowering times of closely related species overlapped varied. In 1950--but not in other years--A. saccharinum and A. rubrum overlapped slightly, making natural crossing possible. A. mayrii and A. cappadocicum could have crossed with A. platanoides in 1947 and 1950, but not in 1949 or 1951.

In A. saccharinum, little variation was found in flowering time within a group of native trees; but some planted specimens a mile away flowered 10-15 days earlier. In A. rubrum there was usually 2-4 days' difference in flowering time among different trees; and little constancy in earliness or lateness of flowering was found in individual trees. In A. negundo there was 3-21 days' difference among five female trees, and 2-3 days' difference among four males. The late-flowering females were consistently late.

In A. platanoides, 34 trees were observed for the entire 5 years; 32 of these were in a single row along a road and the other 2 were about half a mile away. These two separate trees always flowered earlier (as much as 2 days) than the trees in the row.

In the row, individual trees differed by 4-9 days in first flowering time. The behavior of these trees can be summed up this way:



Number
of trees

Flowered--

- 4 --early every year.
- 1 --late every year.
- 7 --early 4 years, intermediate 1 year.
- 2 --late 4 years, intermediate 1 year.
- 1 --intermediate 4 years, early 1 year.
- 6 --early or late 2 or 3 years and
intermediate the rest of the time.
- 11 --at different times in different years.

Thus about a third of these A. platanoides trees were not constant in flowering time.

The same row of trees was observed for constancy in sequence of male and female flowering stages. The following sequences were observed:

male-female
female-male
male-female-male
male-male-female
male-female-female
male-male-male
female-female-male
female-male-male

Of the 32 trees--

- 9 had the same sequence all 5 years.
- 4 had the same sequence 4 out of 5 years.
- 10 had the same sequence 3 out of 5 years.
- 7 had the same sequence 2 out of 5 years.
- 2 had a different sequence every year.

Thus for the species as a whole the chances are 2 out of 3 that any tree chosen at random will have the same sequence of male and female flowering stages the next year.

Part of the apparent lack of constancy was probably due to artifact: a small male period of flowering recorded one year might have been missed the next year. Part was also due to the destruction of an entire period of flowering during the winter; sometimes the expected early bloom failed to open.

A S H
(*Fraxinus*)

General

Except for Fraxinus velutina, most of the observed trees were more than 8 inches in diameter. The diameters of the smallest trees observed to flower were:

F. bungeana--2 inches
F. velutina, F. nigra, F. ornus--3 inches
F. americana, F. pennsylvanica--4 inches
F. excelsior--5 inches

Species of the subsection Melioides (F. americana, F. pennsylvanica, F. velutina) are dioecious, with extremely reduced flowers. Since ash trees are wind-pollinated, the flowers of closely related species are similar.

The flowers of F. excelsior (subsection Bumelioides) are structurally perfect, having anthers and pistils. In this species the occurrence of male, female, hermaphroditic, and variable trees has been reported (7). Only male and female trees are found in the Philadelphia area. The males have large anthers and small pistils that normally fail to develop (although one male produced a few seeds one year). The females have large pistils and smaller anthers; the anthers open and shed small amounts of normal-looking pollen. So far this pollen has been nearly ineffective in self- or cross-fertilization.

Small trees observed flowered heavily or not at all. They flowered over the entire crown. However, two large trees had variable flower crops, and they were localized on certain branches. It is probable that these trees laid down buds over the entire crown, but that a large proportion of the buds were winter-killed. This is known to have occurred on the lower parts of the tree.

Phenology

The phenology of the principal ash species is shown in figure 1. A few additional data show that F. chinensis and F. oxycarpa flower at about the same time as F. pennsylvanica; that F. nigra and F. quadrangulata flower at about the same time as F. excelsior--or 2-3 days later; and that F. ornus flowers a week or more after F. pennsylvanica.

The receptive period (from flower-bud opening until withering of the stigma) lasted 7-10 days for individual female trees and 2-3 weeks for a species. Differences of 3-4

ASH (FRAXINUS)

PENNSYLVANICA AMERICANA EXCELSIOR

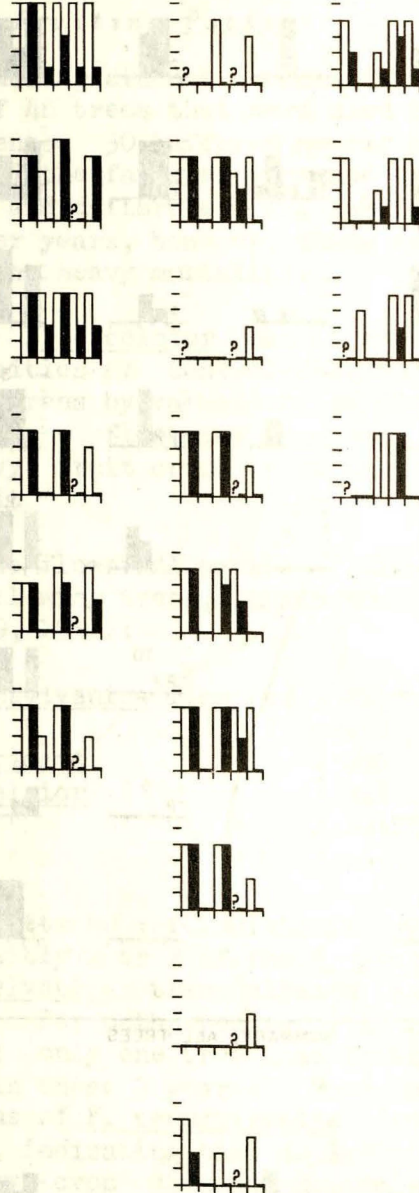
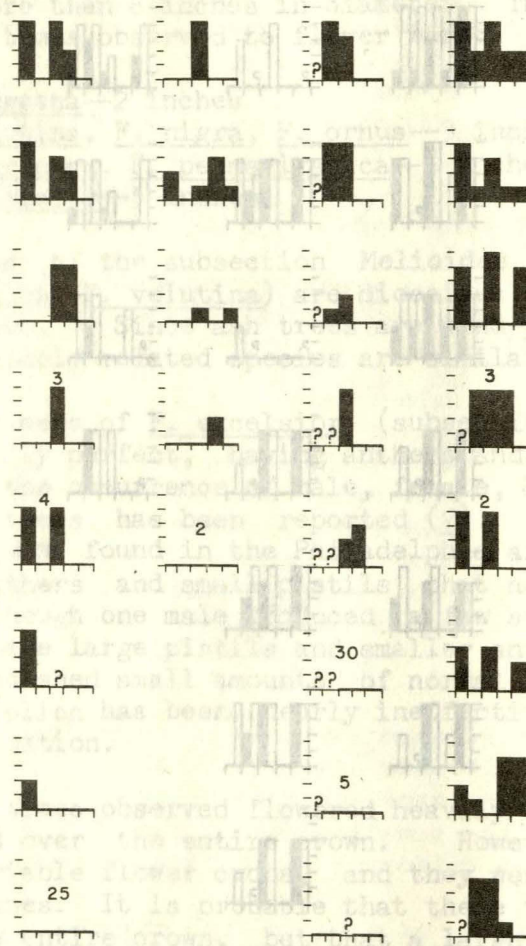


Figure 3.--Flowering and fruiting records of individual ash trees. White bars indicate flowering, black bars fruiting. Height of bars indicates size of crop.

ASH (FRAXINUS)

AMERICANA EXCELSIOR PENNSYLVANICA



SUMMARY, ALL TREES



Figure 4.--Fruiting records of individual ash trees in the Philadelphia area, 1947-51.

days between individual trees were not constant from year to year, but larger differences of 1-2 weeks were. Most of these larger differences were associated with location of the trees, although some were probably associated with geographic origin of the planting stock.

Flowering And Fruiting Pattern

Heavy flowering did not necessarily mean heavy fruiting (fig. 3). Of 48 trees that were used in controlled pollination experiments, 30 suffered nearly complete seed-crop failures. In 1947 the failures were due to a late May frost that defoliated and deflorated all ash trees in low-lying areas. In other years, however, there was no such obvious explanation for the heavy mortality.

Only from F. excelsior has it been possible to get appreciable quantities of control-pollinated seed from normally unfruitful trees by variations in technique. In this species, bagging the flowering branches after pollination resulted in heavy fruit crops even though the rest of the tree bore no fruit.

Data on the flowering habits of male trees are available for the following trees, which were observed for 3 years (1948, 1949, 1951):

9	<u>F. pennsylvanica</u>	flowered	3 out of 3 years.
1	"	"	2 out of 3 years.
4	<u>F. americana</u>	"	1 out of 3 years.
2	<u>F. excelsior</u>	"	3 out of 3 years.
1	"	"	2 out of 3 years.
1	"	"	1 out of 3 years.

Fruiting patterns of individual trees are shown in figure 4. Possibly 2 or 3 of the F. americana and 5 or 10 of the F. pennsylvanica trees classed as nonfruiting are actually males. For both species 1947 and 1949 were the best fruit years; only one tree that fruited in other years failed to fruit in those 2 years. More than a third of the fruiting specimens of F. pennsylvanica fruited heavily 2 or 3 years in a row, indicating that depletion of food reserves by a previous heavy crop does not determine fruiting periodicity. Nor does size of the flower crop (fig. 3).

The ratios of total trees to fruiting trees (at least 2 years out of 5) are 4 to 1 for F. pennsylvanica and 7 to 1 for F. americana. Thus, in a tree-breeding program one should plant 4 or 7 times as many trees as are needed for female parents. Roguing of the unfruitful trees can take place at diameters of about 6 and 8 inches respectively.

Observation for three successive years should be enough to accomplish the roguing and to establish which trees are males.

OAK

(*Quercus*)

No continuous observations were made on the flowering of the oaks. Controlled pollinations were made in 2 years --1947 and 1949. Of 17 trees worked (all bore heavy crops of female flowers), only 4 matured appreciable quantities of either control-pollinated or open-pollinated acorns. Casual observation of other oaks substantiates the general conclusion that heavy flowering does not indicate heavy fruiting.

Most of the trees studied were more than 1 foot in diameter, and open-grown. Heights of these trees were as follows: *Quercus alba*, 30-60 feet; *Q. bicolor*, *Q. macrocarpa*, and *Q. palustris*, 40 feet or more; *Q. borealis* and *Q. lyrata*, 35 feet or more; and *Q. imbricaria*, *Q. phellos*, and *Q. velutina*, 50 feet or more.

Few observations were made in 1949; so most of the records are for only 4 years. For the white oaks (*Q. alba*, *Q. bicolor*, *Q. lyrata*, and *Q. macrocarpa*) 1947 was the best year for the species as a whole and for most individual trees. Only a few specimens fruited well in an additional year (fig. 5).

Fruiting patterns of the black oaks differed from those of the white oaks and also among themselves. More of the trees fruited well in 2 or 3 years. Except for *Q. phellos*, the peak years did not correspond to white oak peak years either in flowering or in acorn ripening. There were many differences in fruiting pattern both among species and among individuals, some of which fruited best in an otherwise off season.

Fruitfulness is especially important to the tree breeder who is working with oaks. Yields of control-pollinated acorns are poor at best. Emasculation is time-consuming, and each flower yields but a single seed. Working 2,000 pollination bags per man-season (6- x 14-inch bag, enclosing 8-10 inches of branch) would be a laudable accomplishment. And work of this intensity would yield 8,000, 4,000, 400-2,000, 200, and 40 acorns respectively from trees bearing very heavy, heavy, medium, light, and very light fruit crops.

The yields to be expected from working 2,000 bags per year--20 bags for each of 10 crosses on each of 10 trees--are listed in table 1.

Table 1.--Expected acorn yield of oak species
from working 2,000 bags

Species	Average annual acorn yield	Number of crosses yielding--	
		4 or more acorns	40 or more acorns
Q. alba	570	19	7
bicolor	320	14	5
borealis	410	12	9
imbricaria	2,000	55	35
lyrata	50	4	0
macrocarpa	590	25	11
palustris	210	10	4
phellos	690	27	14
robur	40	0	0
velutina	220	8	4

Faulty technique (so far, bagging technique has reduced rather than increased seed set) and lessened fertility in interspecific crosses would reduce these yields. Less-than-annual flowering would increase them.

The unfruitfulness of the oaks--and the possibility that selection for fruitfulness may mean selection against vigor--necessitates different breeding procedures for the oaks than those used for other genera.

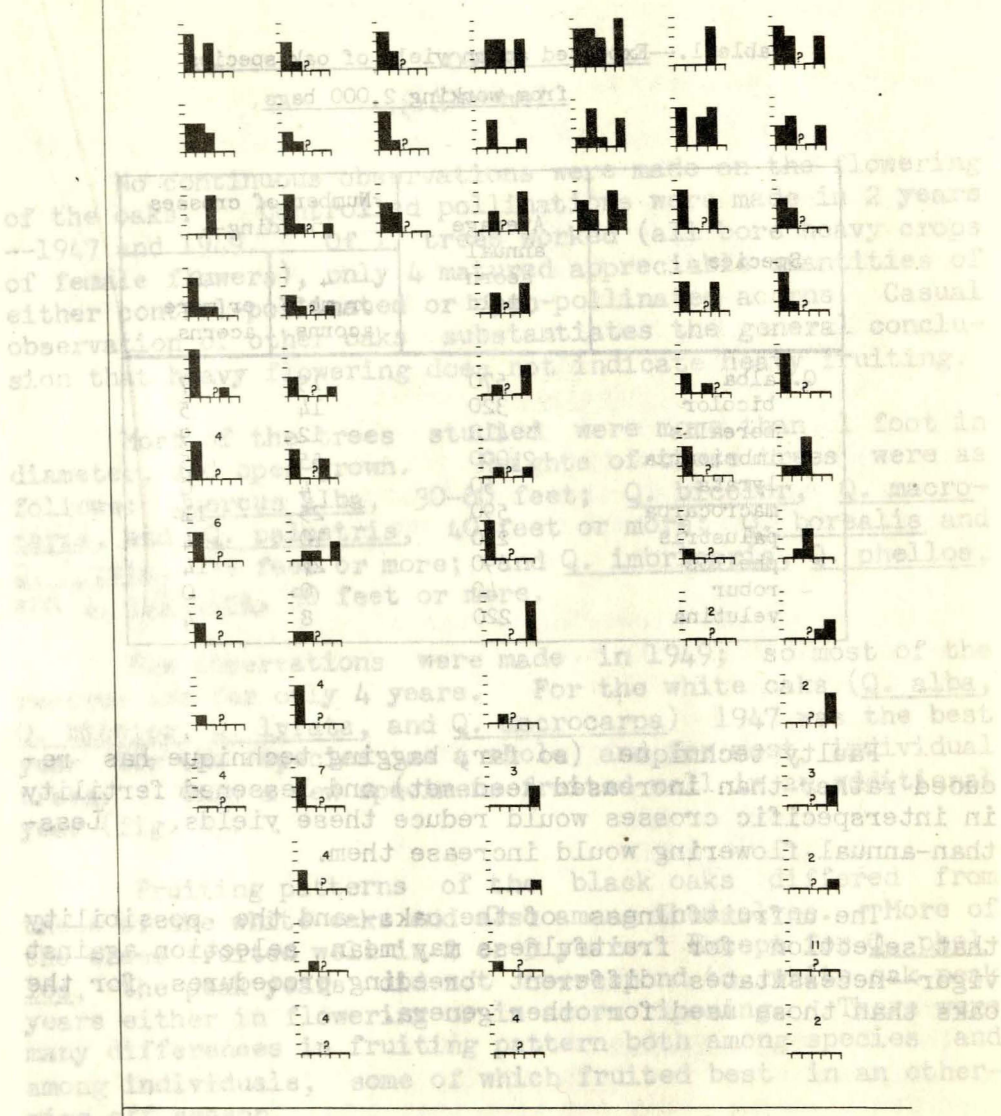
F I R (*Abies*)

Fir trees bear female flowers in the topmost crown and male catkins over the entire crown. One exception in this respect is a very broad-crowned specimen of Abies homolepis: it bore numerous cones at the ends of long lateral branches only 8 or 10 feet from the ground.

The flowering dates of several fir species are shown in figure 1. Data for two A. veitchii trees not included in

OAK (QUERCUS)

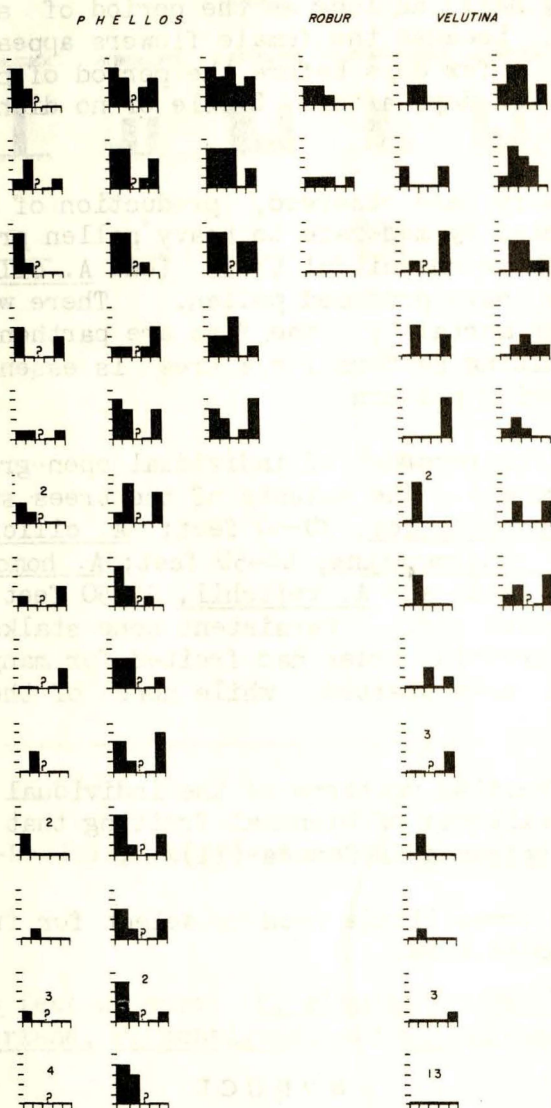
ALBA BICOLOR BOREALIS IMBRICARIA MACROCARPA PALUSTRIS



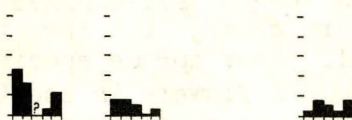
SUMMARY, ALL TREES

Fruitfulness is especially important to the tree breeder who is working with oaks. Yields of control-pollinated crosses are shown in Figure 5. The highest yields were obtained from crosses of *Q. macrocarpa* and *Q. imbricaria* in 1947 and 1948. The lowest yields were obtained from crosses of *Q. alba* and *Q. palustris* in 1947 and 1948. The yields of control-pollinated crosses are shown in Figure 5. The highest yields were obtained from crosses of *Q. macrocarpa* and *Q. imbricaria* in 1947 and 1948. The lowest yields were obtained from crosses of *Q. alba* and *Q. palustris* in 1947 and 1948.

OAK-CONTINUED



SUMMARY, ALL TREES



the figure indicate that this species flowers about the same time as A. lasiocarpa. The flowering periods shown coincide approximately with the period of pollen-shedding. This is usually only half as long as the period of apparent female receptivity, because the female flowers appear, scales already open, a few days before the period of pollen-shedding and close a few days after. Little or no dichogamy was observed.

In every case observed, production of female flowers was accompanied by moderate to heavy pollen production. In addition, three unfruitful trees (one A. cilicica and two A. veitchii) have produced pollen. There was relatively little flower mortality; the firs are parthenocarpic (17). Thus the fruiting pattern for a tree is essentially similar to its flowering pattern.

Fruiting records of individual open-grown trees are shown in figure 6. The heights of the trees studied were as follows: A. cephalonica, 30-60 feet; A. cilicica, A. lasiocarpa, and A. nordmanniana, 40-50 feet; A. homolepis, A. numidica, 30-40 feet; and A. veitchii, 25-50 feet. These trees were 40-50 years old. Persistent cone stalks showed that most of the fruiting trees had fruited for many years before observations were started, while none of the nonfruiters had.

The fruiting patterns of the individual trees do not show the consistency of biennial fruiting that is characteristic of A. balsamea in Canada (11).

There seems little need to select for fruitfulness in the Philadelphia area.

SPRUCE

(*Picea*)

Flowering Habits

Norway spruce (*Picea abies*) bears its female flowers over its entire crown, but they tend to be more abundant in the top. All other spruce species in the Philadelphia area bear their female flowers in the top one-third of the crown. In all species the male flowers are borne over the entire crown.

The heights of the trees studied were as follows: P. abies, P. asperata, P. maximowiczii, P. orientalis, and

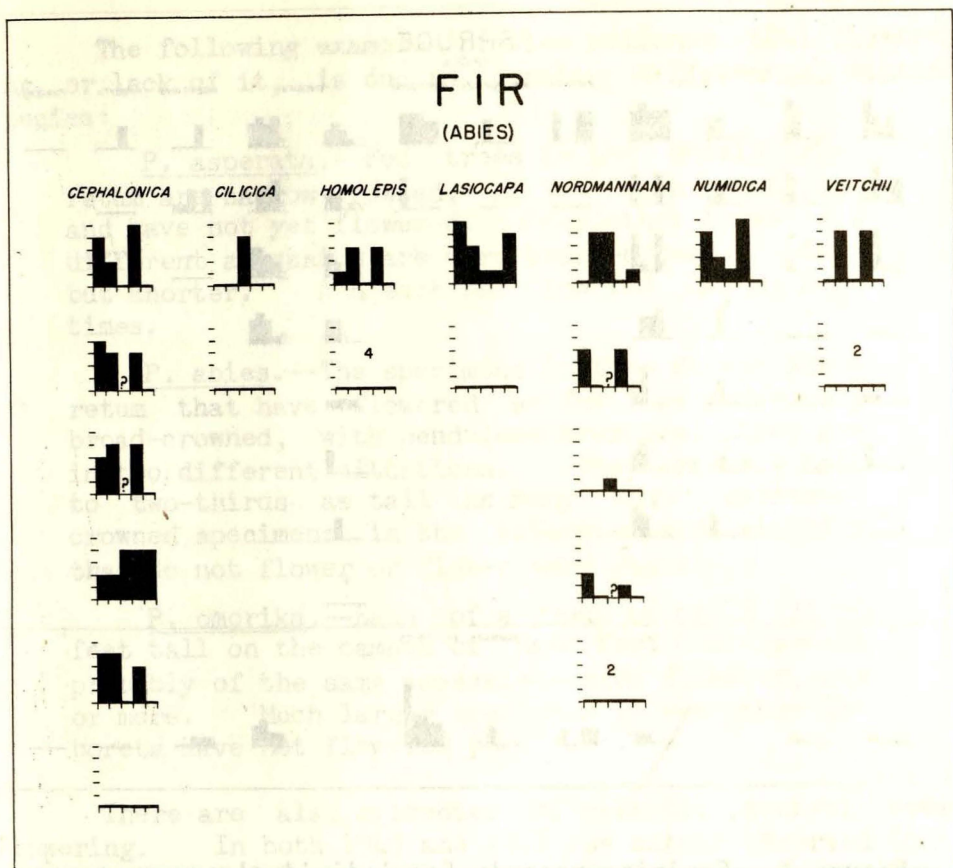


Figure 6.--Fruiting records for individual fir trees.

P. pungens, 30 feet or more; P. glauca, P. omorika, 15 feet or more; P. mariana, P. montigena, and P. polita, 12 feet or more.

Light cone crops were observed on 3- to 8-foot trees of P. abies, P. glauca, P. polita, and P. asperata that had been transplanted a year or two earlier. In each case the fruiting was not repeated; so it was presumably due to a temporary shock stimulus. But in general, transplanting does not seem to be a reliable method of inducing flowering in this area, and many other similarly transplanted trees have not fruited early.

In this area all spruce trees mature at least 75 percent of their female flowers into cones. Thus the female flowering patterns of individual trees are identical to the fruiting patterns (fig. 7).

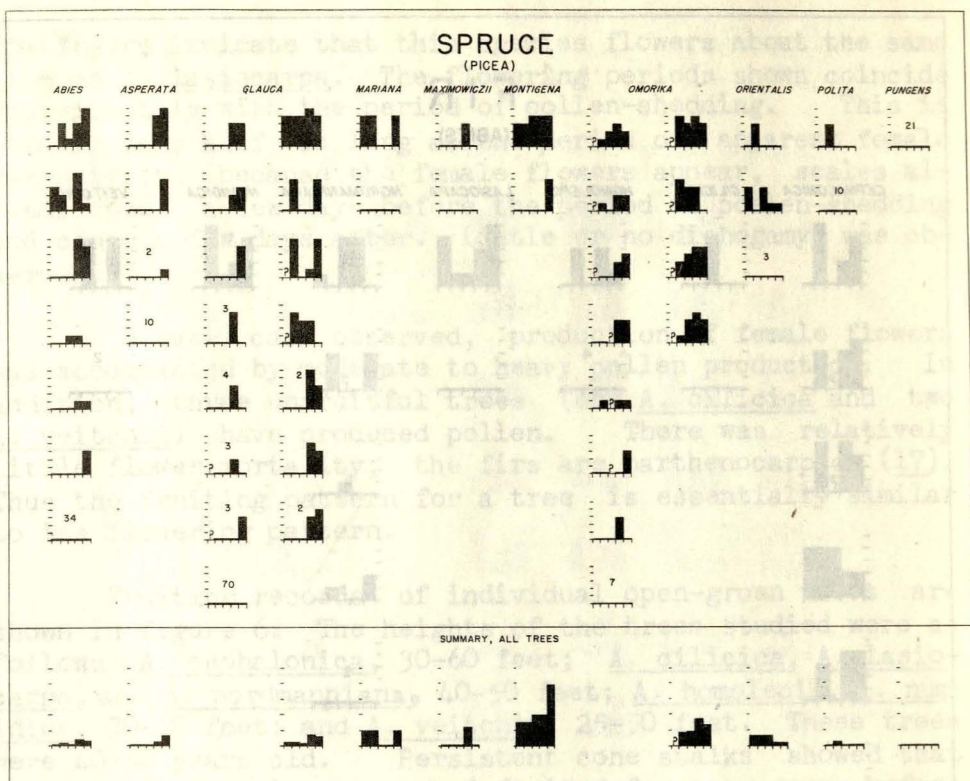


Figure 7.--Fruiting records for individual spruce trees.

Except for a few trees of *P. orientalis*, *P. asperata*, *P. maximowiczii*, and *P. glauca*, pollen was borne only by the fruiting trees. Years of female flowering did not correspond closely to years of male flowering for individual trees. On the whole there were about twice as many female flower crops as male.

So far, available specimens of *P. mariana*, *P. polita*, and *P. pungens* have produced no pollen. Pollen crops of *P. glauca*, *P. omorika*, and *P. orientalis* have been so light that it has been very difficult to collect enough for control-pollination experiments, and very little seed has set to open pollination, even on trees growing in groups (17). Only specimens of *P. abies*, *P. asperata*, *P. maximowiczii*, and *P. montigena* have produced moderate amounts of pollen. Even in these species seed set of nonisolated trees can be increased several times by additional pollination.

The following examples provide evidence that flowering, or lack of it, is due to genetic differences within species:

P. asperata.--Four trees in the Morris Arboretum are narrow-crowned, of the same accession, and have not yet flowered. Four other trees of a different accession are very broad-crowned, older but shorter. And each has flowered one or more times.

P. abies.--The specimens in the Morris Arboretum that have flowered so far are moderately broad-crowned, with pendulous branches; they are in two different situations. They are only half to two-thirds as tall as many other narrower-crowned specimens in the Arboretum and vicinity that do not flower or flower very lightly.

P. omorika.--Each of a group of trees 15-20 feet tall on the campus of Haverford College--all probably of the same accession--have flowered once or more. Much larger specimens in two other arboreta have not flowered yet.

There are also evidences of climatic control over flowering. In both 1949 and 1951 the author observed that the majority of Colorado blue spruce in Spokane, Washington, were fruiting very heavily, although they were no larger and no thriftier than the nonfruiting specimens in Philadelphia. The same tendency was observed in Norway spruce.

Phenology

Flowering dates of spruce species are shown in figure 1. Additional data indicate that: P. maximowiczii flowers even earlier than P. asperata; P. montigena flowered a day or two earlier than P. glauca in 1951; and P. koyamai and P. orientalis flower later than P. omorika.

By bringing male catkins into the laboratory and letting them shed on paper it has been possible to hasten pollen-shedding by only 2 or 3 days. But so far it has not been possible to use as male parents species that flower more than 2 or 3 days after the species used as female parent.

In P. abies the flowering period for individual trees lasts 10 days to 2 weeks. This is because there is a succession of female flowers, each of which remains receptive for about a week. The pollen-shedding period is similarly extended. Differences in flowering time between individual

trees are slight.

In all other species the female and male flowering periods each last 3 or 4 days per tree; they overlap by 25 to 50 percent. At any one time, all the flowers on a tree are within a day of each other in their stage of development. Individual trees differ from each other by a day or two.

No data were obtained on the constancy of phenological differences within species from year to year.

Fruiting Pattern

The fruiting patterns of individual open-grown trees are identical to the patterns of female flowering. There is in spruce a greater tendency toward annual fruiting than in any other group except some of the maples. Many specimens fruited well 4 or 5 years in a row.

In the common species, 1950 and 1951 were the best fruit years, both for the species and for individual trees. For *P. glauca* one reason for this was that many of the trees fruited for the first time in 1950.

In all species the ratio of total to fruitful trees is large. For *P. glauca* this ratio will undoubtedly be reduced as the trees grow older and more come into flower. To establish a breeding arboretum for spruce in this region one should plant 5-10 times as many trees as are needed for female parents.

PINE (*Pinus*)

Flowering Habits

In most pine species, both male and female flowers are borne over the entire crown. However, female flowers were found to be most plentiful in the upper part of the crown. Male flowers were less plentiful--or lacking--in the few uppermost whorls.

In *Pinus strobus*, *P. cembra*, and *P. koraiensis* female flowers were localized in the upper several whorls, including the leader. Male flowers were localized in the upper half of the crown--excluding the few uppermost whorls. The female flowers always and the male flowers generally were

borne on vigorous branches exposed to full sunlight. But in P. strobus appreciable numbers of male flowers were found on shaded inner branches.

Male flowers always occurred on the basal portions of the current year's growth, female flowers at the apical portions of the current year's growth. However, on a few P. thunbergii some or all of the male flowers were replaced by female flowers. The resultant cones were normal--if not crowded. When crowded (sometimes there were 50 or more per shoot), they developed to less than half normal size and did not open properly.

Effect Of Age

The minimum flowering ages of 39 pine species growing in the Eddy Arboretum at Placerville, California, vary from 1 to 13 years (3). Of 19 species grown in both Placerville and Philadelphia, all but three start to flower later in Philadelphia. (P. virginiana flowers earlier, P. banksiana and P. sylvestris at about the same time.) The earlier flowering at Placerville is not associated with greater vigor, for several of the species are equally or more vigorous in Philadelphia.

The approximate heights at which pine species start to flower in appreciable quantity in Philadelphia are as follows: P. densiflora and P. mugo, 3 feet; P. banksiana, P. pungens, P. sylvestris, and P. thunbergii, 5 feet; P. armandi, P. cembra, and P. parviflora, 15 feet; P. cembroides, P. nigra, P. resinosa, P. strobus, and P. taeda, 20 feet; P. koraiensis, 20 feet or possibly much higher; P. flexilis and P. griffithii, 30 feet or more.

There is evidence in three species that minimum flowering age is influenced by provenance. Some 30-foot P. cembra specimens probably of Central European origin have not flowered; but some 12-foot specimens of probable Siberian origin have flowered. In P. flexilis the one tree that has flowered most consistently and most heavily is a runty specimen that differs from all other trees of the species in the area. A group of rather slow-growing straight Scotch pine probably of Scandinavian origin have not yet flowered (20 years after outplanting), but specimens of other origins have.

In their early flowering years, all P. strobus trees observed were exclusively or principally female, bearing up to 400 female flowers but no or few male flowers. Female-ness still predominates among the older trees 1-2 feet in

diameter, although most of these trees do produce small to moderate amounts of pollen.

In P. densiflora also there is a tendency toward femaleness in the first 2 or 3 years of flowering. Precocity of female flowering was also observed in a few younger specimens of P. armandi and P. griffithii.

In P. sylvestris young trees less than 20 feet tall were principally either male or female; most older trees were hermaphroditic. Schrock (15) found that most of the 13-year-old progeny of early-blooming Scotch pine were exclusively male or female. However, according to Gal'pern (4) exclusively male or female trees are rare, although different parts of the tree may be exclusively of one sex.

P. koraiensis was precociously male. Of 6 trees up to 25 feet tall that have flowered, only one has produced a single female flower.

Flower production increased with size of tree in nearly all species. The increase was least in P. strobus. In this species cones are borne only in the upper crown, and the area of the crown suitable for cone production does not increase greatly with age. Some trees produced 200 to 300 female flowers their first year, which is not exceeded by most older trees.

Date of flowering was correlated with taxonomic affinity. Species of Insignes flowered first, of Lariciones next, and of Strobi last. There was sufficient overlapping between species of the same series to make nearly all intra-series crosses possible--except for P. tabulaeformis, which flowered earlier than any other species in the series Lariciones (with most of which it does not cross well) and was difficult to match with males of other species in the series. However, the overlapping in flowering frequently required selection for flowering time in one or both species.

Phenology

Flowering dates of pine species are shown in figure 1. Additional data show that P. monticola (a single specimen) flowers about the same time as P. strobus; that P. koraiensis and P. armandi flower a few days later; and that P. cem-broides flowers a week or two later.

For individual trees the period of pollen-shedding lasted 2-5 days, and the period of female receptivity (from bud opening to scale closing) lasted up to a week, or

slightly longer. All flowers on the tree were within a day or two of each other in stage of development. Sometimes there was a difference of 1 or 2 days in the start of female and male flowering, but there was always enough overlapping to make selfing probable.

Within species there was 3-5 days' difference in onset of flowering between early and late trees. The differences were nearly as great within any small group as within the Philadelphia area as a whole; and they tended to remain constant from year to year.

Flowering And Fruiting Pattern

For medium and larger trees, the following ratings were used for female flower and fruit crops:

<u>Flowers or cones</u> <u>per tree</u>	<u>Rating</u>
10	Very light
10-50	Light
50-100	Medium
100-400	Heavy
Over 400	Very heavy

Actual counts were made only on some of the trees used in controlled pollination work. In P. strobus the ratings were approximately the same for trees of all sizes, but in other species an allowance was made for size.

In nearly all species there were so many instances of heavy mortality between flowering and cone ripening that the size of the flower crop was not a useful indicator of size of cone crop. Data from control-pollination work show that in almost no case was cone mortality due to lack of pollination. Nor was it due to obvious environmental factors--except for some trees of P. densiflora and P. griffithii, in which the flowers were damaged by insects.

(During the period of observation covered by this report, the author assumed that the white pine weevil attacked the cones of P. strobus only during the second year, after the cones had enlarged appreciably; so weeviled cones were counted as sound in estimating heaviness of fruiting. However, in later observations--in 1952 and 1953--conelets dead and dying early in their second year were examined on planted trees near Philadelphia and on wild trees in the Pocono Mountains. All conelets examined had suffered weevil damage and soon dropped. In the areas worked, cone crops were nil in both years even though about half the trees had flowered heavily. Yet control-pollinated branches that were continuously protected by sausage casings did mature cones. It

PINE (PINUS)

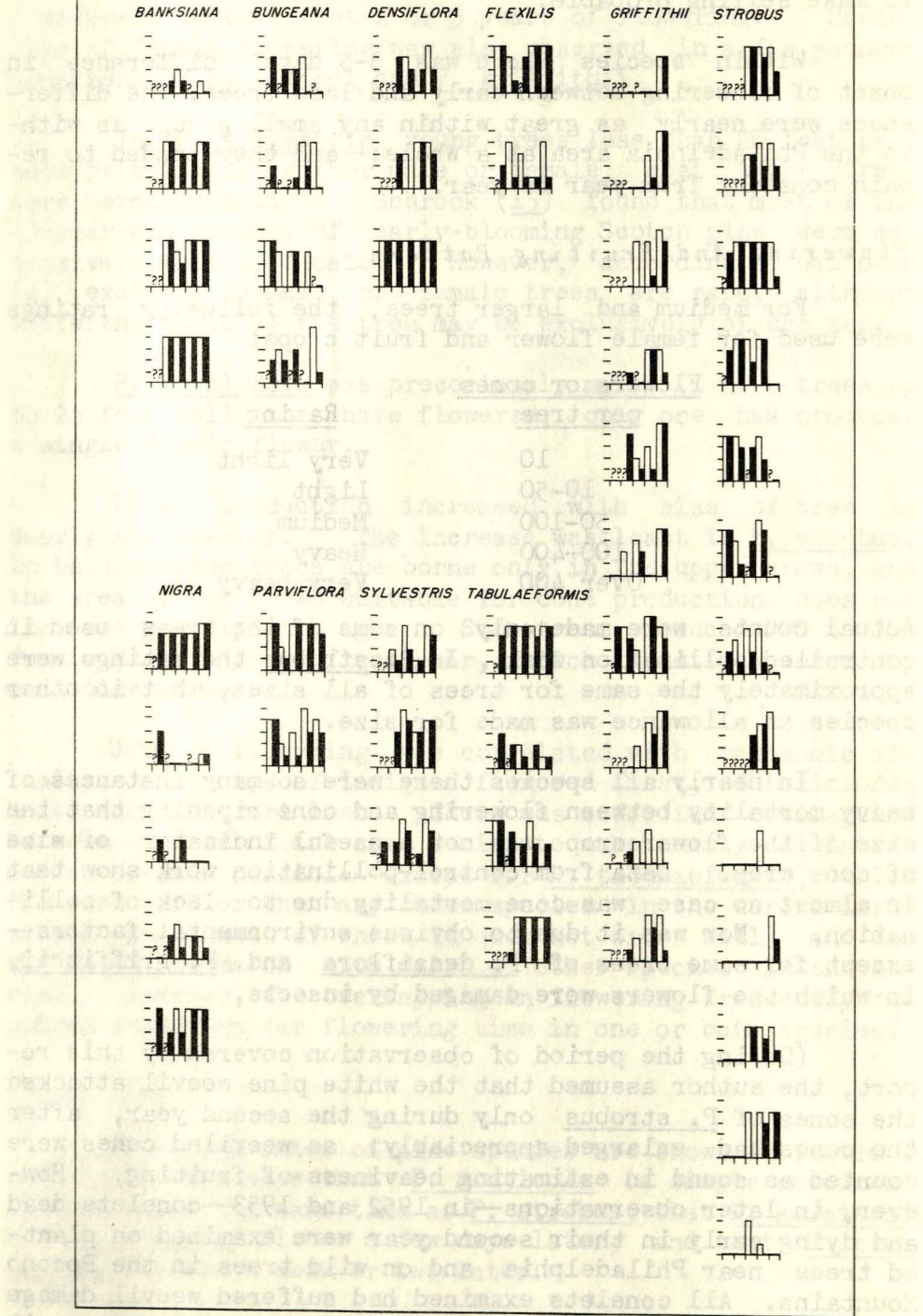


Figure 8.--Flowering (white bars) and fruiting (black bars) of individual pine trees.

appears that in this species the weevil is the principal cause of cone-year periodicity--at least in eastern Pennsylvania. These later observations did not change the conclusions reached for other species.)

Most pine species are generally regarded as bearing heavy fruit crops at intervals of 2 or more years, with light crops or no crops at all in intervening years. This is not the pattern exhibited by most pine species in Philadelphia (fig. 9). More apparent is a tendency for certain trees to maintain heavy cone production year after year.

Of the species included in figure 9, only P. griffithii has what might be called a "seed-year" pattern; and this is not noticeable in the two young trees. A "seed-year" pattern was also observed in P. resinosa. This was not included in the figure because before 1951 observations were limited to a few trees (different each year) that were flowering. In 1951, however, all trees of a large group produced heavier cone crops than were noted on any of the trees in the previous 4 years.

The tendency for certain trees to fruit heavily consistently has been noted by others in studies of Scotch pine (12) and loblolly pine (13).

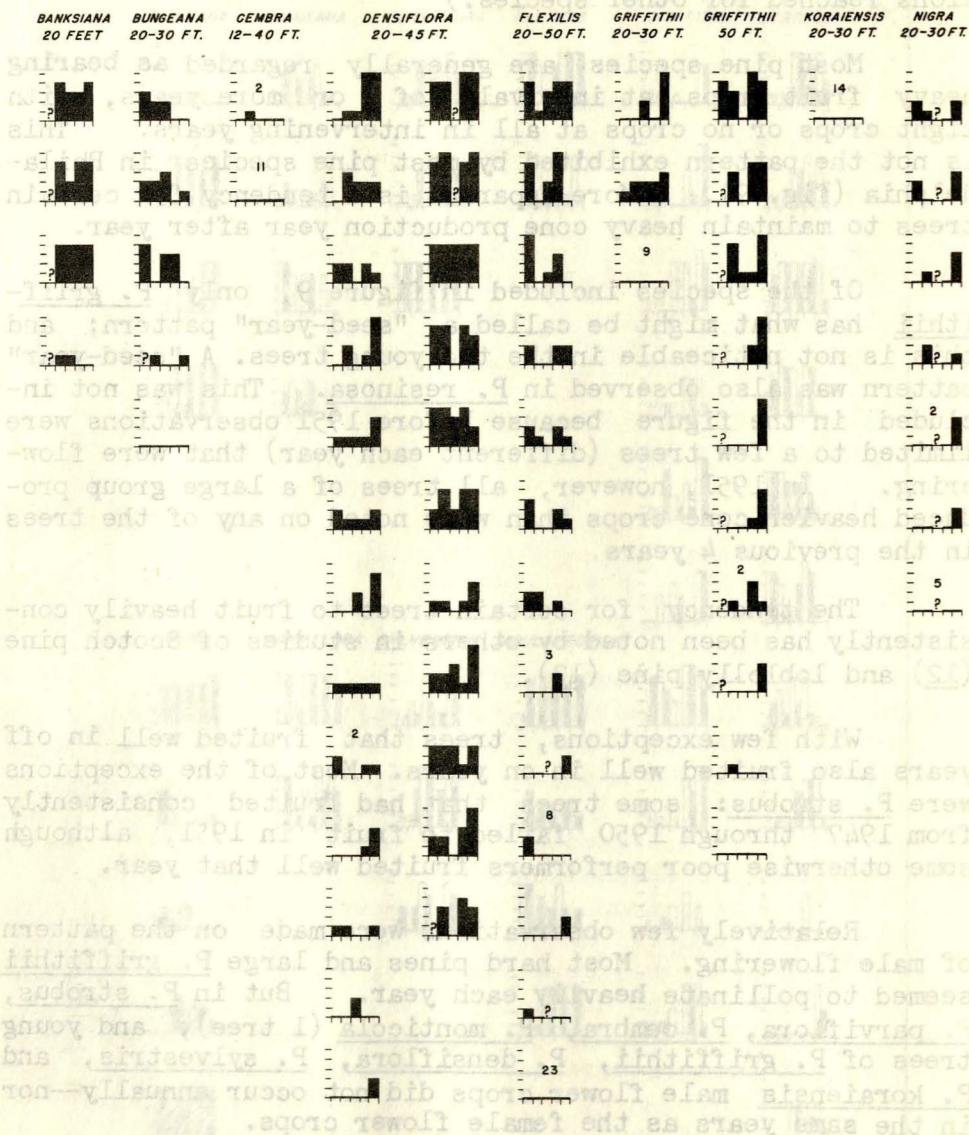
With few exceptions, trees that fruited well in off years also fruited well in on years. Most of the exceptions were P. strobus: some trees that had fruited consistently from 1947 through 1950 failed to fruit in 1951, although some otherwise poor performers fruited well that year.

Relatively few observations were made on the pattern of male flowering. Most hard pines and large P. griffithii seemed to pollinate heavily each year. But in P. strobus, P. parviflora, P. cembra, P. monticola (1 tree), and young trees of P. griffithii, P. densiflora, P. sylvestris, and P. koraiensis male flower crops did not occur annually--nor in the same years as the female flower crops.

Practical Application

Two years' casual observation in Western States indicates that the early fruiting of pines in the West is not maintained in later years by Insignes, Lariciones, and Strobi, the groups that are adapted to the Northeast. Austrian pine seems slightly more fruitful in the West and P. strobus in the East. But the differences are much smaller than in the spruces. For the present more attention should be given to "vegetative climate" than to "cone-producing climate" in establishing breeding arboreta and seed orchards.

PINE (PINUS)

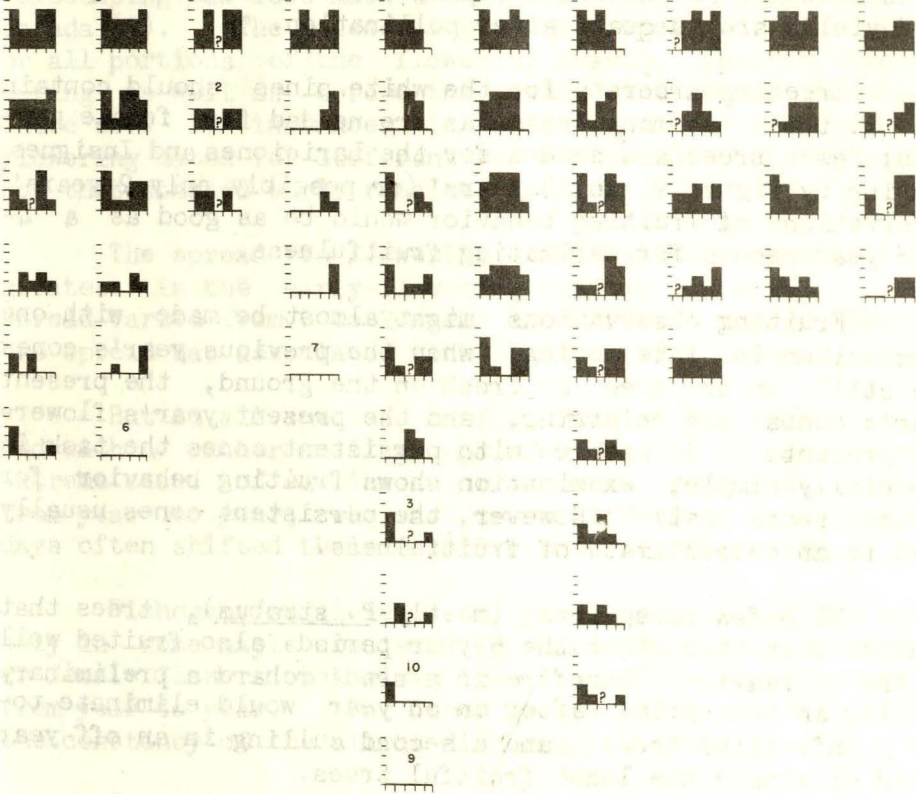


SUMMARY, ALL TREES

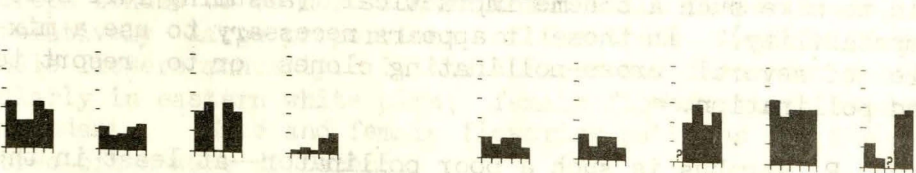
Two years' casual observation in Western States indicates that the early fruiting of pines in the West is not maintained after years of heavy fruiting. In the Northern States the groups that are adapted to the West and P. strobus pine seems slightly more fruitful in the West and P. strobus in the East. But the differences are much smaller than in the species. For the present more attention should be given to "vegetative climate" than to "cone-productive climate" in establishing breeding stock and seed orchards.

PINE-CONTINUED

NIGRA 50 FT. PARVIFLORA 12-30 FT. PUNGENS 12-20 FT. PONDEROSA 20 FT. STROBUS 20-40 FT. STROBUS 40 FT. SYLVESTRIS 20-50 FT. TABULAEFORMIS 15-20 FT. VIRGINIANA 15-35 FT.



SUMMARY, ALL TREES



However, seed yield per cone is important. In *P. strobus* yield per cone is much lower in the Philadelphia area than in other parts of the species' range. Seed yields are also low in *P. parviflora*, *P. flexilis*, and certain trees of *P. griffithii*. Seed orchards of these species should not be established in the Philadelphia area. In other species seed yields are adequate after pollination.

Breeding arboreta for the white pines should contain 5 to 10 times as many trees as are needed for female parents; fewer trees are needed for the *Lariciones* and *Insignes*. Judging by figure 9, any 3 years' (or possibly only 2 years') observations of fruiting behavior would be as good as a 4- to 5-year record for estimating fruitfulness.

Fruiting observations might almost be made with one examination in late spring, when the previous year's cones are still on the tree or fresh on the ground, the present year's cones are enlarging, and the present year's flowers are present. In species with persistent cones the task is especially simple; examination shows fruiting behavior for several years past. However, the persistent cones usually lead to an overestimate of fruitfulness.

With few exceptions (mostly *P. strobus*), trees that fruited best throughout the 5-year period also fruited well in the on years. Therefore in a seed orchard a preliminary culling in the spring after an on year would eliminate totally unfruitful trees, and a second culling in an off year would eliminate the least fruitful trees.

One scheme for mass-producing hybrid seed calls for interplanting selected male and female clones. This appears feasible if either *P. strobus* or *P. sylvestris* is used as the female parent, for in both species there are enough essentially female clones--at least in youth--to give hybrid seed with little contamination by selfing.

The same may also be true of young *P. griffithii* and *P. densiflora*. However, most hard pines are sufficiently male to make such a scheme impractical (assuming full self-compatibility). In these it appears necessary to use a mixture of several cross-pollinating clones or to resort to hand-pollination.

P. strobus is such a poor pollinator--at least in the Philadelphia area--that it seems advisable to use this species only as a female parent for mass-production of seed in the next 30 or 40 years. Only old trees already on the site can be used as male parents.

GENERAL CONCLUSIONS

There was a slight telescoping of the over-all flowering season in years when flowering started late. This telescoping was less marked than that found farther north in Canada (9). The telescoping was not equal for all species or all portions of the flowering season, because weather during as well as before the season influenced flowering. There were few instances in which the curves representing flowering dates for different years crossed: that is, a season that started early remained early.

The spread in flowering time within species was greatest in the early-flowering maples and ashes. This spread varied from 0 to 2 weeks in different years. Much of the spread was associated with location of the trees.

But in all species half or more of the spread occurred within rather small groups of trees. In most species extreme cases of earliness or lateness remained constant from year to year, whereas trees differing by only a few days often shifted their relative order in flowering.

Dichogamy sufficient to preclude selfing was noted only in some maple species, in which the precocity of male or female flowers on a given tree tended to remain constant from year to year. For other groups there are few data on the constancy of the slight dichogamy observed.

In table 2 these phenological data for the Philadelphia area are compared with data from three other locations. As the flowering season at northern locations is telescoped, one should expect the differences between locations to be greatest for the earliest species. This trend is obvious only for A. saccharinum, the very earliest. For the later species differences between locations bear little relation to flowering time.

In the maples, ashes, and most hard pines male flower crops tended to be more common than female flower crops, and relatively large proportions of the trees tended to bear male flowers annually. In the spruces and firs, and particularly in eastern white pine, female flower crops were more abundant. Male and female flowering patterns for the same tree often were different.

Sugar maple, the ashes, some oaks, red pine, and P. griffithii exhibited a strong tendency toward having very good and very poor seed years. In other species a tendency for certain trees to bear consistently heavy or light fruit

Table 2.--Number of days species in three other localities
flower before (+) or after (-) the same species
in the Philadelphia area

Species, in order of flowering	Placerville, California	Central Wisconsin	Ottawa, Ontario
Acer saccharinum	--	-19 to -21	-21 to -29
A. negundo	--	+ 2 to - 9	--
A. platanoides	--	0 to -10	--
A. saccharum	--	- 3 to -19	- 8 to -31
Pinus tabulaeformis	+10 to +26	--	--
P. banksiana	+24 to +41	- 1 to -16	--
P. virginiana	- 3 to + 9	--	--
P. resinosa	+19 to +22	--	--
P. sylvestris	+19 to +20	--	-10 to -13
P. thunbergii	+29 to +33	--	--
P. nigra	+13 to +16	--	--
P. bungeana	+24 to +32	--	--
P. flexilis	+14 to +27	--	--
P. griffithii	+24 to +25	--	--
P. strobus	+14 to +21	--	--

Sources: (3, 8, 9).

crops was more pronounced than the tendency toward seed years. Thus the tree breeder is apt to get better results on the average by selecting trees rather than years. With relatively few exceptions, fruiting in off years was confined to specimens that made good showings in other years.

In the maples and spruces there was little mortality between flower and fruit; the size of the flower crop governed the size of the fruit crop. In many pines, and particularly in the ashes and oaks, large flower crops were unreliable as indicators of large fruit crops. In few cases was it possible to determine the cause of mortality or to forecast mortality except by average performance of the tree in the past.

In many of the groups, performance of the tree in an off year gave a reliable estimate of its performance over a 5-year period. Presumably selection could be practiced without recourse to long-continued fruiting observations. In nearly all cases a preliminary culling in an on year, followed by another culling in an off year, would be quite as effective as culling based on a continuous 5-year record.

Little correlation was found between occurrence of good seed years in different species, even though closely

related and flowering at the same time. Presumably any attempt to correlate fruiting behavior with weather conditions would involve a minutiae of detail to avoid arriving at an explanation that suited only one species.

UNFRUITFULNESS ---

CONSEQUENCES AND REMEDIES

Unfruitfulness is common in sugar maple, ashes, oaks, spruces, and many pines. Most trees of these species failed to fruit adequately in a 5-year period. This is apparently due in large part to genetic factors, since nearly all the trees observed were open-grown and vigorous.

Unfruitfulness has not been a serious problem in crop-plant breeding, for two reasons. First, most crop plants are annuals or short-lived perennials. Natural selection has continually favored types that produce seed every year. Second, the fruit itself is of value. Improved fruitfulness has been one of the principal objectives of the breeding work, and not merely a side line.

But with trees, natural selection has favored fruitfulness only to the extent that a tree produces good seed several times during a long life. There has been little artificial selection.

With trees, natural selection has favored fruitfulness much more in species that are characteristic of the initial stages of succession than in those species that belong to climax associations. Pioneer species such as jack pine, silver maple, poplars, and elms, which closely follow fire or flood and must have large seed supplies ready on short notice, are much more fruitful than the sugar maple, beech, and oaks of the climax forest.

Effects On Research

Unfruitfulness presents a serious technique problem. It also presents some broader implications. The principal consequences of unfruitfulness are:

- The improvement program is delayed. In the work of the Northeastern Forest Experiment Station there have been numerous instances in which it has been impossible to make or repeat a desired cross in 5 years, in spite of a seeming abundance of breeding material.

- In the nut trees, the fruit itself is in demand. Selection for fruitfulness will in itself result in desirable new varieties.
- There is a probability, not yet tested, that excessive fruitfulness and lack of **vigor** are associated. This is most likely in the oaks and other species in which a large fruit crop means a heavy drain on the tree. It may be that the selection for fruitfulness necessary for control-pollination work will in itself invalidate any improvements expected from the breeding.
- Emphasis is shifted away from desired economic qualities.
- The numerical basis for selection is reduced.

Extrapolation of the results of crop-plant breeding leads one to believe that most of the characters believed to be important in tree breeding--vigor, branchiness, pest resistance--will prove to be controlled by multiple factors. If so, the improvement possible by selection within species will depend on the number of trees the selection is based on.

From populations of 10, 100, and 1,000 trees we can expect to recover individuals 1.28σ , 2.33σ , and 3.10σ above the population mean in one character. Or, if we consider a population of 1,000 trees on which we practice selection for 1, 2, 3, or 4 different characters simultaneously, we can expect to recover trees that are 3.10σ , 1.86σ , 1.28σ , or 0.92σ above the population mean with respects to those 1, 2, 3, or 4 characters. These figures apply to phenotypes. Since phenotype and genotype are usually imperfectly correlated, the genotypes will be even closer to the mean.

To illustrate how this selection works in practice: Take a population of 2,000 trees and select the best 10 percent from the upper end of the phenotype-distribution curve. If there is a fairly good correlation between phenotype and genotype, these 200 trees will all be from the upper end of the original genotype-distribution curve. By means of progeny tests the 10 percent giving the best offspring can be selected from these 200 parents.

If the species is so unfruitful that only 10 percent of the trees fruit, the original population is thus reduced to 200 and the best 2 of 200 trees have been selected rather than the best 20 of 2,000. And 2 trees are not so firm a foundation for a new variety as 20 trees.

Or, the rigorousness of the selection can be relaxed so there still are 20 selected parents; but the gain in performance may be so slight it cannot be measured.

If one starts with an original population of 200 trees, of which only 10 percent are fruitful, one can select only for fruitfulness, for selection for other characters will be very inefficient in so small a population.

Also, in much interspecific crossing work the success of the work will depend on selection of the best individuals within the parent species.

Lessening The Effects

There are four ways the undesirable consequences of selection for unfruitfulness can be avoided or lessened:

- Adjust the breeding program to avoid the necessity of selecting for fruitfulness. With the oaks even a medium-scale control-pollination program would involve rigorous selection for fruitfulness. This is laborious and might invalidate selection for other characters. With material of average fruitfulness it would be far easier to make 1-parent progeny tests on 500 trees than to make 2-parent tests on 10 trees. Although the 1-parent test is a much less precise measure of combining ability than the 2-parent test, it would uncover a greater amount of good germ plasm among 500 than among 10 trees.
- The precision of the 1-parent test could be improved considerably by planting the preliminary phenotypic selections in such a manner that all are subject to pollination by the same pollinators. This approximates the top-cross used in testing corn inbred lines in which a mixture of several standard lines is used as the pollen parent.
- Induce fruiting artificially. In recent years there has been a great interest in induced fruiting in northern Europe. Preliminary results are favorable (1, 2). However, induced fruiting must be permanent, or the treatment must be capable of repetition year after year to be most effective. Such fruiting as was noted in a few spruce trees after transplanting would not be very practical in a breeding program.
- Locate breeding arboreta and seed orchards in regions of maximum fruitfulness. This is common prac-

tice in agriculture, where seed production is concentrated in limited areas known to be favorable. As noted, certain spruce species fruit much better in the West than in the East. With further study, more examples can be expected where breeding arboreta and seed orchards should be located apart from the regions of vegetative testing and use.

- Increase the population on which selection is based. The number of trees needed per species or per race will usually be much larger than can be handled in the conventional arboretum with a wide **spacing** between trees. However, most species will at least start to fruit on a close spacing such as is used in ordinary forest planting. There is no reason why the functions of the test planting and the breeding arboretum should not be combined. In all probability there can be considerable culling for poor vigor, branchiness, and pest susceptibility by the time fruiting starts in earnest.

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